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RESEARCH ARTICLE

Ecological niche differentiation between *Acanthodactylus micropholis* and *A. khamirensis* (Sauria: Lacertidae) in southern Iran

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ABSTRACT. *Acanthodactylus micropholis* Heidari, Rastegar-Pouyani, Rastegar-Pouyani & Rajabizadeh, 2013 and *A. khamirensis* Blanford, 1874 are genetically and morphologically distinct, but their ecological differentiation has not previously been evaluated. The ecological niche models of these two sister species *Acanthodactylus* were reconstructed using climate and geographical data. Species distribution modeling for *A. micropholis* and *A. khamirensis* was used to make predictions and showed that most parts of southern and southeastern Iran are suitable for the distribution of both species. Habitat suitability was mostly dependent upon minimum temperature of the coldest month and seasonal precipitation for *A. micropholis* and *A. khamirensis*, respectively. Niche similarity tests (niche overlap and identity tests) were performed to evaluate species differentiation based on the ecological species criterion. Our results indicate that both species have different ecological niches and are significantly separated from each other. Therefore, our study corroborates previous analyses based on molecular and morphological evidences that suggested that *A. micropholis* and *A. khamirensis* were valid species.

KEY WORDS. Ecological species concept, fringed-toed lizard, Iranian Plateau, precipitation, temperature.

INTRODUCTION

Species delimitation is a great challenge in biology (Wiens 2007), because biologists base it on a variety of different criteria, such as morphology, phylogeny, anatomy, acoustic, biology and ecology (De Queiroz 2007). Different species are adapted to their habitats and are also isolated from each other by post- or prezygotic barriers (the biological species concept) (Mayr 1978). In some cases, the biological species concept is insufficient to describe the true relationship between species, meaning that more criteria are needed to confirm the separation of the gene pool of a given species from other species (Templeton 1989, Jones 2003, Baker and Bradley 2006). Recently, new methods in molecular phylogeny, morphology, and ecology have been developed that aid in greater clarification of species separation (Schlick-Steiner et al. 2010, Fujita et al. 2012). According to the ecological criterion, each species occupies its own ecological niche space and cannot allow other species to enter the space (Van Valen 1976). To examine whether species occupy distinct niche spaces, ecological niche models (ENMs) have been used in which bioclimatic variables are used to compare species spaces and to find the degree of niche overlap between them (Peterson et al. 1999, Wiens 2004, Raxworthy et al. 2007, Barve et al. 2011). Speciation occurs when two populations are isolated from each other genetically and ecologically, after which they consequently develop morphological differentiation (Wiens 2004). Because morphological differentiation appears at the final stage, it is important to evaluate molecular and ecological differentiation as well.

Lacertid lizards of the genus *Acanthodactylus* have a wide distribution range from North Africa through the Middle East and Iranian Plateau (Tamar et al. 2016). So far, eight species of this genus have been recorded from Iran (Safaei-Mahroo et al. 2015). Recently, the genus has been revised using molecular phylogeny (Heidari et al. 2014) and a new species, *A. khamirensis*, was described as belonging to the "*micropholis*" species complex (Heidari et al. 2013). In both species description papers, morphological and molecular markers confirmed the specific level of the newly described species. However, it is still important to examine the ecological niche separation of these lizards for more confirmation.

In this study, the ecological niche differentiation between two species (*Acanthodactylus micropholis* Blanford, 1874 and *A. khamirensis* Heidari, Rastegar-Pouyani, Rastegar-Pouyani & Rajabizadeh, 2013) was examined. Also, modeling was used to predict the potential distribution of both species in south of Iran

and the degree of niche space overlap between them. Finally, we discuss important abiotic factors (temperature and precipitation) affecting geographic isolation and niche differentiation based upon ecological niche modeling.

MATERIAL AND METHODS

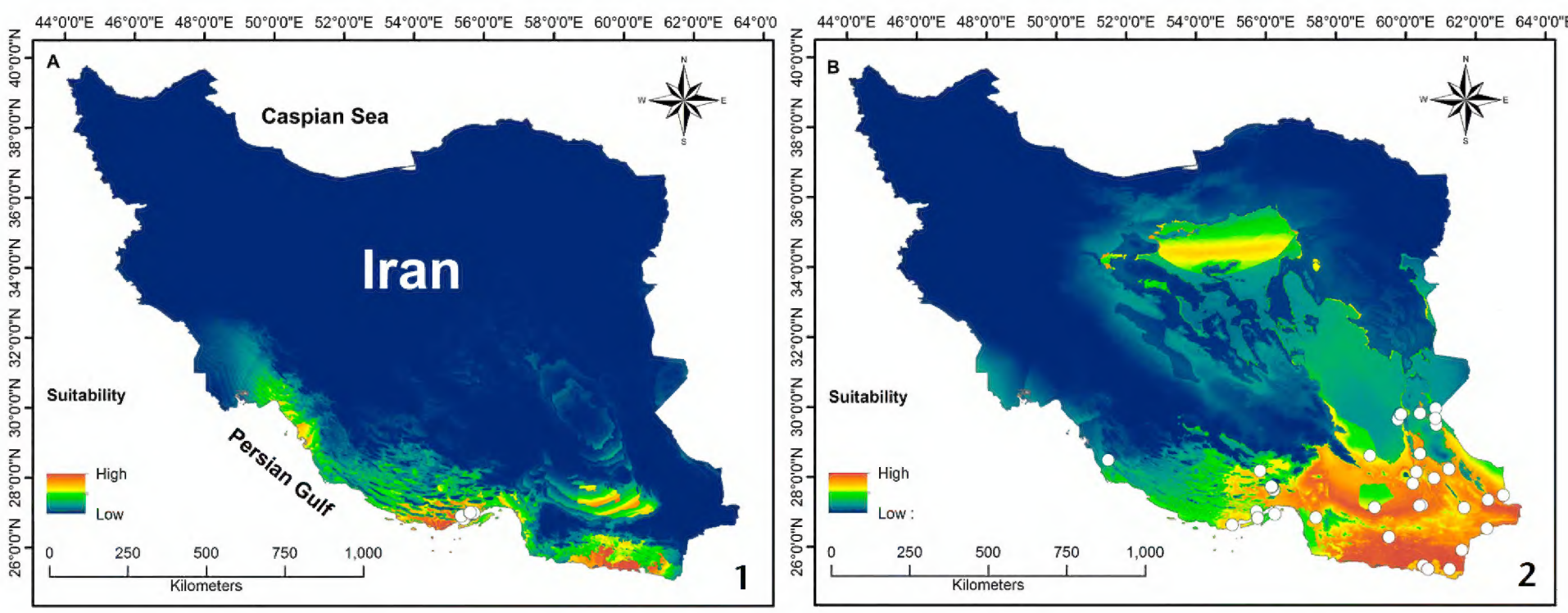
All occurrence records of both species were obtained from the literature (Heidari et al. 2013, 2014, Šmid et al. 2014). In total, 45 presence records belonging to both species (nine records for *A. khamirensis* and 35 records for *A. micropholis*) (Appendix 1) were used. In total, 19 bioclimatic variables were downloaded from the WorldClim website (Hijmans et al. 2005) in 30 arc-second resolution. All layers were clipped using ArcGIS 10.3 (ESRI) for the Iranian boundaries. To elucidate the autocorrelation relationship between variables, Openmodeller v. 1.0.7 (de Souza Muñoz et al. 2011) was employed. Relevant grid values for each variable were extracted and imported into SPSS v. 16.0, then analyzed for the bivariate-correlation Pearson coefficient. Variable pairs with correlation ≥ 0.7 were removed from the analyses. Finally, six bioclimatic variables were selected for analyses as follows: BIO3 (Isothermality); BIO6 (Minimum Temperature of Coldest Month); BIO9 (Mean Temperature of Driest Quarter); BIO12 (Annual Precipitation); BIO15 (Precipitation Seasonality); BIO17 (Precipitation of Driest Quarter). Maxent 3.4.1 (Phillips et al. 2018) was used to predict the species distribution suitability in combination with presence records and climate layers (Elith et al. 2011). In total, 70% of data were used as training data and 30% were set as test data. Other parameters were left as default, including: maximum 500 iterations, convergence threshold 10^{-5}, regularization multiplier 1 and 10 replicates with cross-validation method (Phillips et al. 2018). Model accuracy was evaluated by area under the curve (AUC), which ranged between 0.5 (the predicted model is not better than random points) and 1 (the predicted model is very good); AUC > 0.9 is very good and > 0.8 is good (Swets 1988).

To assess the niche differentiation of two species, niche overlap and niche identity tests were examined based on the habitat suitability scores from SDM (Warren et al. 2010). ASCII files were employed by ENMTools 1.3 (Warren et al. 2010) to obtain the percent of niche overlap and niche identity. To validate the percent of niche overlap and niche difference, two criteria were used: Schoener's *D* (Warren et al. 2008) and Hellinger's-based *I* (Schoener 1968). Schoener's *D* calculates the suitable range based on the probability of occupied grid cells. Hellinger's-based *I* work similarly to Schoener's *D* but without its assumption (Warren et al. 2010). These indices ranged between 0 (complete divergence/no overlap) and 1 (high similarity/complete overlap).

RESULTS

Based on the occurrence records, the distribution range of two species overlapped. Predicted models confirmed the species distribution in southern Iran (Figs 1, 2). AUC values of the models varied from 0.981 ± 0.015 (mean and standard deviation) to 0.893 ± 0.027 for *A. khamirensis* and *A. micropholis,* respectively. The model predicted suitable habitat for *A. khamirensis* in southern coastal regions of Iran from Bushehr province to Sistan-Baluchestan province. The regions included in the prediction near Bandar-e Lengeh reflect the current distribution pattern of the species, but predictions of suitable habitat in Bushehr and Sistan-Baluchestanare outside of the current distribution of the species (Heidari et al. 2013, Šmid et al. 2014) (Fig. 1).

Habitat suitability for *A. micropholis* was distinctly focused on southeastern Iran, reflecting the current distribution pattern of the species (Heidari et al. 2014, Šmid et al. 2014) (Fig. 2). One



Figures 1–2. Predicted potential distributions of *A. khamirensis* (1) and *A. micropholis* (2), generated by MaxEnt. Three main colors show habitat suitability on the map. Warm colors refer to the high suitability level.

Table 1. Relative importance and percentage of contribution of variables used in MaxEnt model for *A. khamirensis* and *A. micropholis*. The most contributed variables for each species are in bold.

Description of variables	Percentage of contribution (%)	
	A. khamirensis	*A. micropholis*
Isothermality	0.3	–
Minimum temperature of coldest month	–	61.7
Mean temperature of driest quarter	2	1
Annual precipitation	–	24.2
Precipitation seasonality	85.1	–
Precipitation of driest quarter	12.6	13.1

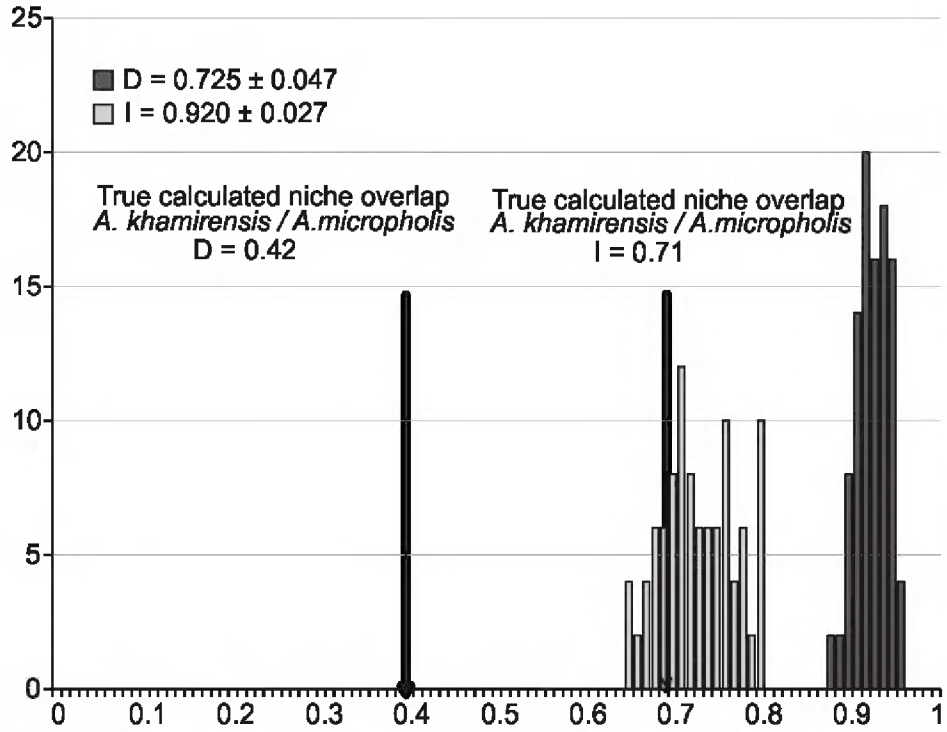


Figure 3. Results of the identity test. Black arrows refer to the actual niche overlap as calculated by ENMTools (*D* and *I*). The bars (with two different patterns) are calculated by replicates with identity test mode.

of the presence records of *A. micropholis* was situated outside of the predicted suitable range in Bushehr province (Kamali 2013). This point is far from the western most records of the species in Hormozgan province, suggesting that it could represent a misidentified specimen. The percentage contribution of each bioclimate variables indicated that the greatest contributions to the models were from the minimum temperature of coldest month for *A. micropholis* and from precipitation seasonality for *A. khamirensis* (Table 1).

Niche overlap between *A. khamirensis* and *A. micropholis* indicated that their niche similarity was lower than 0.5 (Hellinger's-based $I = 0.713$ and Schoener's $D = 0.426$) supporting the recognition of both taxa at the specific level. The identity test indicated that the null hypothesis regarding niche overlap can be rejected and the two species are distinctly differentiated in their ecological niches. The result of the niche identity test (Fig. 3) showed that predicted niche models for *A. khamirensis* and *A. micropholis* were completely separate ($D_{H0} = 0.725 \pm 0.047$ vs. $D_{H1} = 0.420$ and $I_{H0} = 0.920 \pm 0.027$ vs. $I_{H1} = 0.710$) (Fig. 3).

DISCUSSION

The notion of evolutionary lineages diverging by occupying different niches is the basis of one of the oldest species concepts (Ecological Species Concept – ESC, Van Valen 1976). Nakazato et al. (2010) suggested – based on SDM analyses of wild tomatoes – that environmentally mediated differentiation, rather than simply geographical isolation, can be the major driving force in species divergence.

Recently, the genus *Acanthodactylus* was revised and a new species from the *A. micropholis* complex was described (Heidari et al. 2013). *Acanthodactylus khamirensis* is distributed in the westernmost part of the range of *A. micropholis* (Šmid et al. 2014). Although molecular and morphological differentiation of these species was indicated by Heidari et al. (2014), differences in ecological niche occupancy was not reported until the current study.

The habitat suitability prediction for *Acanthodactylus micropholis* in southeastern Iran showed that its distribution pattern completely covered the predicted area (Fig. 2), but a larger area in southern Iran was predicted for *A. khamirensis* (Fig. 1). These two species have different ecological requirements, because habitat suitability for *A. khamirensis* is mostly dependent to the precipitation, but habitat suitability for *A. micropholis* is primarily dependent on minimum temperature (Table 1). Niche overlap between the two species is low and they are differentiated from each other based on several abiotic factors. Here, this separation has been confirmed and the true calculated niches are far from the hypothesized niches (Fig. 3). The evidence suggests that precipitation seasonality in Hormozgan province can influence the vegetation type of the region, which might provide more suitable conditions for *A. khamirensis* presence. On the other hand, habitat suitability for *A. micropholis* is mostly dependent on minimum temperature in winter. This environmental variable may define time of hibernation (Mayhew 1965) and affect the activity period of the species.

The present study indicates ecological niche divergences between the two spiny-toed lacertids of the genus *Acanthodactylus* and these results corroborate previous molecular and morphological conclusions (Heidari et al. 2014), suggesting that the two species are also valid based on the ESC.

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Appendix 1. Records used to predict the habitat suitability of *Acanthodactylus khamirensis* and *A. micropholis*.

Taxon name	Longitude	Latitude
Acanthodactylus micropholis	55.717	27.017
	60.450	27.200
	60.382	27.179
	60.200	27.817
	59.517	26.283
	62.350	27.350
	60.867	29.500
	60.850	29.967
	62.783	27.483
	61.233	28.233
	61.667	27.117
	60.400	29.817
	60.800	27.967
	61.250	25.367
	60.400	28.667
	58.967	28.617
	59.100	27.133
	61.600	25.917
Acanthodactylus micropholis (continued)	60.300	28.150
	62.317	26.533
	55.750	26.833
	56.241	26.945
	57.425	26.836
	55.016	26.632
	55.822	28.182
	56.217	27.634
	60.834	29.672
	59.767	29.650
	51.473	28.490
	56.166	27.715
	56.165	27.717
	56.149	27.730
	60.494	25.469
	60.630	25.365
	59.853	29.796
Acanthodactylus khamirensis	55.645	26.987
	55.506	26.978
	55.502	26.934
	55.354	26.928
	55.414	26.825
	55.339	26.911
	55.596	26.990
	55.700	26.998
	55.588	27.010

Continues

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